Morphological characters of the immature stages of *Henotesia narcissus* (Fabricius, 1798): description and phylogenetic significance (Lepidoptera: Nymphalidae, Satyrinae, Satyrini, Mycalesina)[1]

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Abstract: Development and morphological characters of the immature stages of *Henotesia narcissus* (Fabricius, 1798) from Madagascar were studied. The aims were to find phylogenetically relevant characters to analyze the systematic relationships of the subtribe Mycalesina within the Satyrini and to find criteria for distinction of the larval stages. Clear synapomorphies have been found for Mycalesina and the subtribe Ypthimina in the larval stages such as clubbed setae and thoracic dorsal trichome fields in the last instar larvae. Thus, the close relationship between the Mycalesina and the Lethina/Elymniina as proposed by Miller (1968) is not confirmed by our results. Our conclusion is supported by further common characters of the Mycalesina and Ypthimina which, however, cannot be easily interpreted in phylogenetic terms. Such characters which are not shared by the Lethina and Elymniina are for example the shape of the scoli present on the head capsule in all larval instars, the enlargement of stemma 3 and the complete absence of a cubito-median cross-vein in the pupal wing tracheation. It is shown that the head capsule diameter is a distinctive parameter for the five larval instars of *H. narcissus*. Its developmental increase can be adequately described by an exponential function. Similar mathematical functions can be used also to define the increase in body length and in stemma diameter. These simple calculations may help in the identification of individual larval instars which is necessary for comparative morphological studies.

Morphologische Merkmale der Präimaginalstadien von *Henotesia narcissus* (Fabricius, 1798): Beschreibung und phylogenetische Bedeutung (Lepidoptera: Nymphalidae, Satyrinae, Satyrini, Mycalesina)

Zusammenfassung: Entwicklung und Morphologie der Präimaginalstadien von *Henotesia narcissus* (Fabricius, 1798) aus Madagaskar wurden untersucht. Ziel war es, phylogenetisch relevante Merkmale zu identifizieren, um die systematische Stellung der Subtribus Mycalesina innerhalb der Satyrini zu analysieren und um unterscheidende Kriterien für die verschiedenen Larvalstadien zu finden. Eindeutige Synapomorphien wurden bei den Larvalstadien zwischen den Mycalesina und der Subtribus Ypthimina gefunden wie die keulenförmig verdickten Setae und thorakale dorsale Trichomfelder im L5-Stadium. Somit wird die von Miller (1968) diagnostizierte nähere Verwandtschaft zwischen den Mycalesina und den Lethina/Elymniina durch unsere Untersuchungen nicht bestätigt. Unsere Schlußfolgerungen werden durch weitere gemeinsame Merkmale der Mycalesina und Ypthimina gestützt, die aber phylogenetisch nicht leicht interpretierbar sind. Solche Merkmale, die mit den Lethina und Elymnina nicht geteilt werden, sind zum Beispiel die Form der Kopfkapselscoli, das vergrößerte Stemma 3 und das Fehlen einer cubito-medianen Verbindung bei den pupalen Flügeltracheen. Es zeigt sich, daß der Kopfkapseldurchmesser ein distinkter Parameter für alle 5 Larvalstadien von *H. narcissus* ist. Seine Größenzunahme kann mathematisch adäquat durch eine Exponentialfunktion beschrieben werden. Ähnliche Funktionen können zur Charakterisierung des Längenwachstums des Körpers sowie der Zunahme der Stemmatadurchmesser benutzt werden. Durch einfache Kalkulationen können einzelne Larvalstadien identifiziert werden, wodurch die Vorausetzung für vergleichende morphologische Studien geschaffen ist.

Introduction

The order Lepidoptera includes an estimated number of about 1.4 million species (Gaston 1991, Simon 1996). For many, if not most of the known species often nothing more than some characters of the wing pattern have been published which may allow the identification of the species in the mature stage. Details on adult morphology, immature stages, life-history and information about the rôle in the complex ecological network are lacking for the majority of the tropical species. A good example to demonstrate this status of poor knowledge are the Madagascan species of the Nymphalid subfamily Satyrinae, including the genus *Henotesia* Butler, 1879. In a recent study, however, the phylogeny of the Madagascan Mycalesina has been investigated by means of mitochondrial gene sequences coding for two different cytochromes (Torres et al. 2001).

The genus *Henotesia* comprises 57 known species occurring in continental Africa, Madagascar and some minor Indian Ocean islands (D'Abrera 1980). The majority of species (43) is confined to the island of Madagascar. For these endemics only little information is available, limited to the knowledge of adult wing-pattern in most cases. Exceptions are *H. benedicta* Paulian, 1951, *H. aberrans* Paulian, 1951 and *H. narcissus* (Fabricius, 1798) for which the structures of the male genitalia are figured (Corbet 1948, Paulian 1951). With respect to immature stages, a brief description of the larval stages and pupa of *H. narcissus* has been published by Aurivillius (1911). In addition, a scanning electron microscopic figure of the head capsule surface of the L_1-larva of *Henotesia ankaratra* (Ward, 1870) has been presented by Sourakov & Emmel (1997a). A similar status of knowledge is also found for the 41 endemic species of the genus *Strabena* Mabille, 1877. Only recently, morphological data on the immature stages of three *Strabena* species have been published (Roos 1987a, 1987b). The species of both genera, *Henotesia* and *Strabena,* make up about 82 % of the total Madagascan Satyrinae species.

[1] Publication no. 21 of the Institute for Butterfly Research and Conservation, Bochum. (No. 20: Arnscheid, W., Roos, P. H., Seis, R., & Achtelik, G. (2001): Aktuelle Makrolepidopterenfunde aus dem Ruhrgebiet (2). – Melanargia **13:** 105–116.)

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A slightly better situation is found for the continental species of the genus *Henotesia*. Van Son (1955) and Usher (1985) provided figures of the male genitalia, and more recently an extensive revision has been published for the 11 continental species (Kielland 1994) which unfortunately does not include any information on immatures. However, a detailed description accompanied by excellent figures is given for the immature stages of *H. perspicua* (Trimen, 1873) by van Son (1955). Up to now, these are the only data on immature stages of the genus *Henotesia* which are suitable for comparative systematic and phylogenetic considerations. As a small contribution to fill this gap, morphological characters of immature stages of *Henotesia narcissus* are described in the present paper. They are discussed with respect to their systematic and phylogenetic significance.

Materials and methods

An adult ♀ of *Henotesia narcissus* was collected in the vicinity of Sadikamonjo, Maroantsetra, Madagascar, on 27. iv. 1985 (P. Roos leg.). Keeping the ♀ in a plastic box with grass blades as substrate to stimulate oviposition, a total of 22 eggs was obtained within 3 days. Hatching of the larvae occurred between 5 to 6 days after oviposition. The larvae were reared on grass-species of the genus *Poa*. The time course of the postembryonal development is given in Table 1.

Table 1: Postembryonal development of *H. narcissus* in the breeding experiment.

	Date from–to (1985)	Duration (days)
Oviposition	29. iv.–1. v.	4–5
Hatching	2. v.–6. v.	6–9
1st moult	11. v.–12. v.	4
2nd moult	15. v.–18. v.	6
3rd moult	21. v.–25. v.	6
4th moult	27. v.–29. v.	7
Pupation	4. vi.–9. vi.	10–20
Emergence	14. vi.–29. vi.	

Calculation of the exponential growth characteristic of developmental head capsule increase was done by computer-aided linear and non-linear regression analysis using the software GraphPad Prism™.

Preparation of first instar larvae for examination of the primary setae pattern was done as described by Roos & Arnscheid (1989). Briefly, larvae conserved in 70 % ethanol were treated with 10% NaOH for 2 hours at ambient temperature. The head capsules were removed and the contents of the body was squeezed out by means of fine needles. Subsequently, the preparation was dehydrated by ethanol (70%, 90%, 95% and 100%), transferred into xylol and embedded in Entellan™. Analyses of surface structures of the head capsules by scanning electron microscopy were performed in the Institute for Biophysics and Electronmicroscopy, University of Düsseldorf, Germany.

Preliminary remark: In the present work, the system of Miller (1968) has been used for the Satyridae. However, according to the actual view that the "Satyridae" constitute only a subfamily of the Nymphalidae, the subordinate taxa used by Miller were degraded subsequently so that subfamilies (-inae) became tribes and tribes (-ini) became subtribes (-ina). This principle has been consistently adopted throughout the paper.

Results: Characterization of the immature stages

Eggs

Analysis of the egg structure could not be performed under field conditions. When returning to the laboratory, all the larva had hatched and the egg shells had been consumed by the larvae. The colour of the eggs is light yellow and their surface is only moderately structured. From 1 egg conserved in 70% ethanol the maximum diameter was determined to be 1.04 mm.

The larval stages

Prior to describing the individual larval stages, some general features will be presented with respect to developmental alterations. Basic parameters of all instars such as body lengths, head capsule diameters, lengths of the head and caudal processes and diameters of stemmata 2 and 3 are summarized in Table 2. It is shown in Fig. 1 that the increase in head capsule width (H_x) can be described mathematically by an exponential function of the form $H_x = H_0 * e^{Bx}$, where H_0: extrapolated value for H_x, when x = 0; e = 2,718; B: calculated value defining curvature; x: number of the larval instar. For practical purposes the above equation can be easily transformed to $H_x = H_1 * f^{x-1}$, where H_1: head diameter of first instar larva; f: relation of head diameters of two consecutive instars ($f = H_x/H_{x-1}$); x: number of the larval instar. This equation provides a good approximation which is easily obtained without a computer program. The B- and f-values of both equations are related to Dyar's (1890) ratio r by $r = {}^1/_f = {}^1/e^B$. In a semilogarithmic presentation, the excellent correlation between head diameter and larval instar becomes more obvious. By linear regression analysis, a correlation coefficient of $r^2 = 0.96$ is obtained. The increases in body length and stemmata diameters can be described by similar functions (see below).

Dorsal processes of the head capsule are present in all instars, L_1 to L_5. In contrast to the head diameter, the developmental increase in process length can be adequately described by a linear function. Using linear regression analysis for correlation of process length (LS) versus larval instar, a correlation coefficient of $r^2 = 0.963$ is obtained. The increase in µm is defined by

$L_S = 0.094x + 0.012.$

Colour plate: Figs. 2–6: Larva and pupa of *Henotesia narcissus*. **Fig. 2:** L_1. **Fig. 3:** L_3. **Fig. 4:** L_5. **Fig. 5:** L_5, thorax, dorsal. **Fig. 6:** pupa.

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Table 2: Characterization of larval instars. — [1] Lengths immediately determined after moulting, for L_5 maximum length is given in addition; [2] sm: smooth with a loose network of faint ridges; dp: with scattered ring-shaped depressions. L_1 to L_5 = larval instars 1 to 5. n.d. = not determined; n.p. = not present.

Parameter		Larval	instar			
		L_1	L_2	L_3	L_4	L_5
Body	length (total), mm[1]	n.d.	5.5	7.4	10.0	16.0–23.5
	length of anal scoli, µm	n.p.	250	350	480	430
	length of setae, µm	200	n.d.	50	50	75
Head	width (w), mm	0.66	0.86	1.18	1.71	2.53
capsule	processes length (p), mm	0.10	0.23	0.28	0.35	0.51
	w/p (ratio)	6.60	3.74	4.21	4.89	4.96
	surface structure[2]	sm	dp	dp	dp	dp
	length of setae, µm	230	60	60	50	50
Stemmata	stemma 2 (S2)	31	38	56	77	111
(diameter),	stemma 3 (S3)	38	59	90	128	175
µm	S3/S2 (ratio)	1.23	1.55	1.61	1.66	1.58

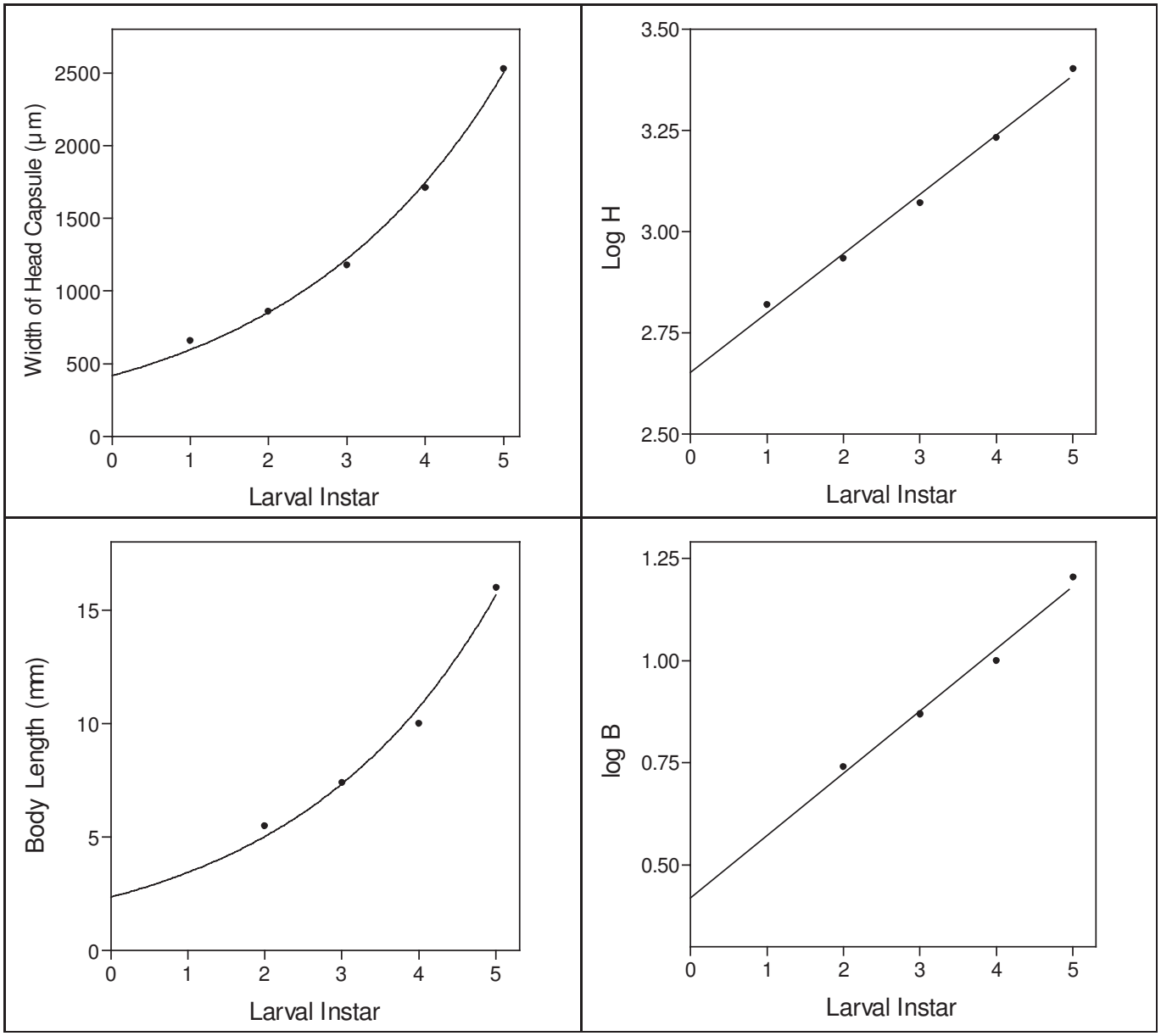

Fig. 1: Increase in larval head capsule width and body length during development presented as exponential growth function and in a semilogarithmic form.

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On each hemisphere, the head capsule bears six stemmata of which stemma 3 is much larger compared to the others (Fig. 12, REM). In Table 2, the diameters of stemma 2 and 3 in all larval instars are given for comparison. The ratio of diameters of stemma 3 and stemma 2 (S3/S2) remains nearly constant for all five instars and is in the range of 1.2 to 1.6. The developmental increase in the diameter of individual stemmata is analogous to the head capsule diameter (Fig. 1). In fact, the exponents B of the growth curves for stemma 2, stemma 3, head capsule diameter and body length are very similar, namely 0.34, 0.36, 0.36 and 0.38, respectively (Table 3), indicating isometric growth characteristics.

Table 3: Growth functions for some characters of the larval instars of *Henotesia narcissus*. x = larval instar. Functions are derived from the original data by linear and non-linear regression analysis.

Character	Exponential growth equation	Linear functions of semilogarithmic presentations and respective correlation coefficients (r^2)
Width of larval head	$H = 417\ \mu m * e^{0.36\ x}$	$\log H = 0.15\ x + 2.65$ $r^2 = 0.994$
Body length	$B = 2.36\ mm * e^{0.38\ x}$	$\log B = 0.15\ x + 0.42$ $r^2 = 0.985$
Diameter of Stemma 2	$S_2 = 20.3\ \mu m * e^{0.34\ x}$	$\log S_2 = 0.14\ x + 1.33$ $r^2 = 0.990$
Diameter of Stemma 3	$S_3 = 29.6\ \mu m * e^{0.36\ x}$	$\log S_3 = 0.17\ x + 1.44$ $r^2 = 0.990$

L_1 larva: The total body length of the freshly hatched L_1-larvae could not be determined under field conditions. By extrapolation, using the growth function of Table 3, a value of 3.4 mm can be calculated. Directly after hatching the body is light creamy coloured and does not show any stripes. As for *H. perspicua* (Trimen, 1873) (see van Son 1955), the ground colour changes to green and some longitudinal stripes develop with the onset of feeding. On the thorax and the first five abdominal segments the dorsal and stigmatal lines are dark green and change to a light brown colour on the caudal segments. The epistigmatal lines are white. Anal scoli are not yet developped.

The head capsule is pitch black with a largely smooth surface (Fig. 2). A network of low ridges is present on the lateral and upper parts only. A spherical protrusion on top of each hemisphere bears the two setae P_1 and P_2 (Figs. 7, 8, 15) and the puncture P_B. Besides this prominent structure, some further scoli of minor size are present which carry the setae L_1, A_3 and O_2. The basis of the remaining setae is only slightly developped except for one with unidentified homology. It is located on the line between AF_1 and L_1 and apical of A_3 and has also been found in the genera *Hipparchia* Fabricius, 1807 and *Erebia* Dalman, 1816 (García-Barros 1987, Roos & Huck 1999). Two punctures, O_B and A_A, are close to the stemmata, with A_A apical of stemma 2 and O_B between stemma 3 and 4. As a special feature, C_1 on the clypeus is missing but is present in later larval stages (Figs. 13, 15). The absence of C_1 has been checked in several specimens by light microsocopy in addition to analysis by scanning electronmicroscopy. F_1 and the punctures F_A are located at the anterior margin of the frons whereby F_1 is even slightly closer to the clypeus than F_A. Structurally, the setae of the head capsule differ from those of the thorax and the abdominal segments (see below) in that they are thin, gradually tapering from the base and ending up in a fine tip. Judged from analysis by scanning electron microscopy, their surface appears smooth.

The shape of the labrum does not differ considerably from that of other Satyrine species examined so far (García-Barros 1987, Roos unpublished). The anterior invagination may be slightly deeper compared to *Hipparchia fidia* (Linnaeus, 1767) of the subtribe Satyrina (García-Barros 1987). The lateral spines are present but only poorly developped (Fig. 7). They become more prominent in later larval stages (Fig. 13).

The primary thoracic and abdominal setae pattern of the first instar larva of *H. narcissus* is shown in Fig. 16. There are some deviations from the Ditrysian ground plan (Hasenfuss 1963). The prothorax of narcissus bears only a single L-seta (L_1) and a very thin and hairlike SD_1 emerging from the body in nearly a right angle, two characters which are shared by the setae of abdominal segment 9. There are several lines of evidence to designate the long slender seta of the prothorax as SD_1 although it is positioned ventrally of SD_2. First, it appears homotypic to the single SD-seta of abdominal segment 9 due to its similar structure. Designation of the latter as SD_1 is clear because, according to Hinton (1946), SD_1 is always present on the ninth segment, whereas SD_2 can be absent in some taxa. Second, SD_1 is in most cases longer than SD_2. Third, SD_1 can be specialized structurally as shown for "Agrotidae" (Hinton 1949) and here for *H. narcissus*. On the meso- and metathorax, two SD-setae are present.

In contrast to other Ditrysia (Wasserthal 1970), D_1 setae of *H. narcissus* are longer than D_2 on all segments (Fig. 17). With respect to their relative positions, D_1 of the abdominal segments is always located anteriorly and dorsally of D_2 whereas on the pro- and mesothorax D_2 lies nearly ventrally of D_1. Except for the prothorax, the dorsal seta D_1 possesses the greatest length compared to the other setae on each segment. Neither microsetae could be detected on the eighth abdominal segment. This, however, does not prove their absence because this segment was only incompletely spread in the preparation.

The surface of the black pigmented setae of both the body and the head capsule is smooth. They end up in a fine tip, except for the thoracic and abdominal XD, D, most SD and some L-setae which end up in a slender club (Fig. 16) which is not pigmented as observed by light microscopy. V, SV and most L-setae of the body are structurally similar to those of the head capsule.

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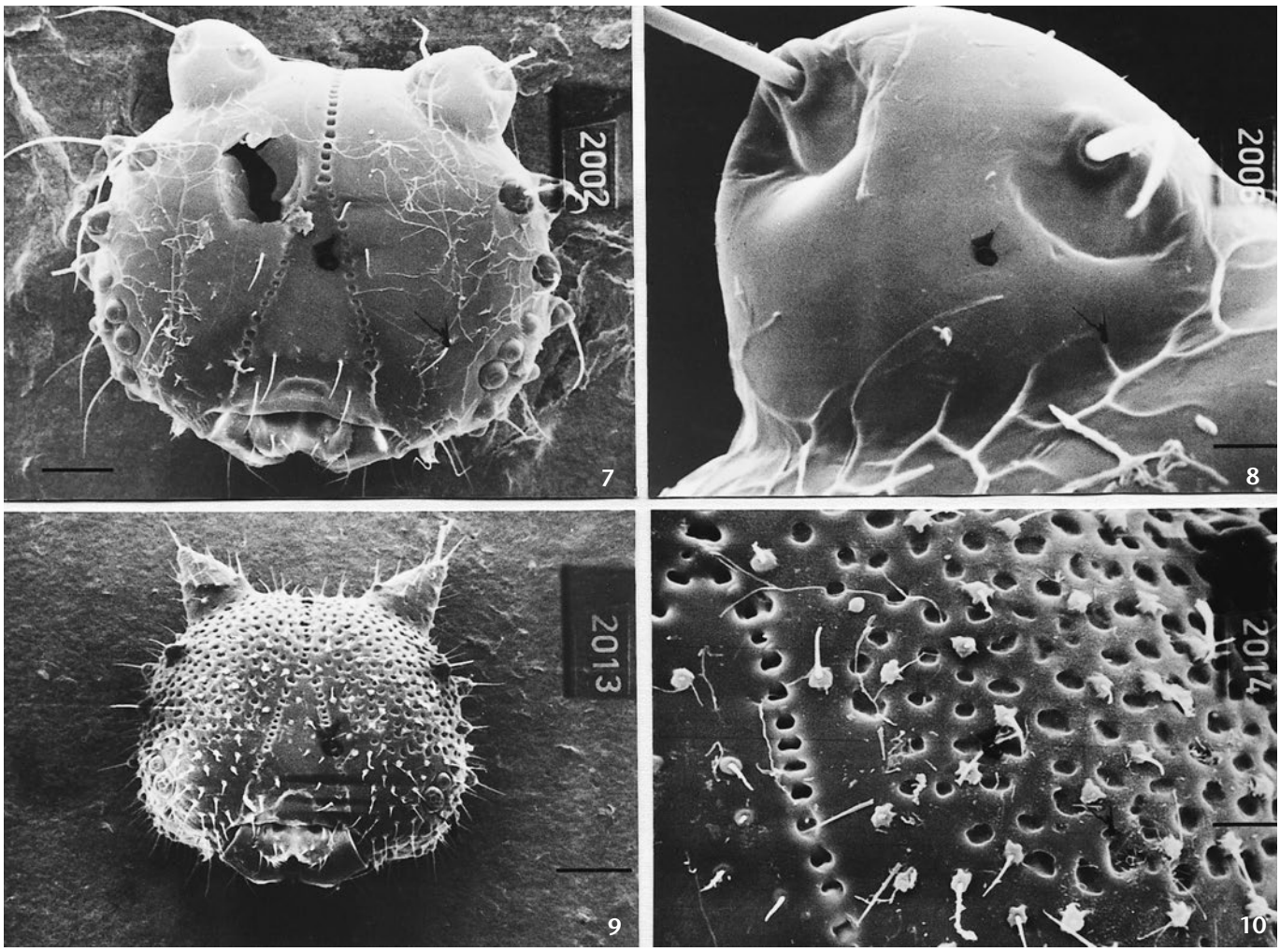

Figs. 7–10: Analysis of the surface structure of the larval head capsule of *H. narcissus* by scanning electron microscopy. **Fig. 7:** L_1, frontal view. **Fig. 8:** L_1, head process. **Fig. 9:** L_2, frontal view. **Fig. 10:** L_2, details of the surface structure; adfrontal suture on the left. — Bars represent: (10) 100 µm, (11) 20 µm, (12) 200 µm, (13) 50 µm.

L_2 larva: Total length of the freshly moulted larvae: 5.5 to 6.2 mm. The colour of the head capsule is still black brown. Its surface structure, however, differs considerably from that of the L_1-larva. Almost the entire surface shows small circular depressions (Fig. 9, 10) which are absent on the frons and the scoli. As is evident from Figs. 9 and 11, the head processes show a conical form and thus also differ markedly from L_1. The setae of the head capsule are structurally similar to those of L_1. Their maximum length amounts to about 60 µm only. The green body wears dark green longitudinal stripes which obtain a light brown colour on the caudal segments. Anal scoli appear in this larval stage and attain a length of about 250 µm. Their dorsal surface shows a reddish brown colour. In contrast to L_1, a great number of secondary setae is present on the thorax and the abdomen.

L_3 larva: Total length (freshly moulted): 7.4 mm. In this instar, the colour pattern of the head capsule and the body is more differentiated than in the former larval stages. The head shows a brownish green ground colour and some darker brown areas which extend to the head processes (Fig. 3). The body is light green with darker longitudinal colour elements, i.e., dorsalis, subdorsalis, epistigmatalis and stigmatalis. On the last 3 segments, dorsalis and stigmatalis are brownish in the caudal parts of these segments. The space between subdorsalis and epistigmatalis is light whitish green. The red coloured anal scoli reach a length of 350 µm. The stigmata are faintly bordered in dark brown colour. Setae of either body and head are colourless and emerge from a white knobbed basis.

L_4 larva: Total length (freshly moulted): 10 mm. The coloration of the head capsule and the body is very similar to L_3. As in L_3, the caudal half of each segment is lighter green than the apical part and the anal scoli are of a red colour. The subdorsal whitish body line, however, is extended onto the head capsule reaching the basis of the scoli. Generally, the whole green body of the larva is covered with numerous white speckles which constitute the basis of the setae. The lengths of the latter do not differ considerably from those of the L_3 instar. Analysis of the stemmata by scanning electron microsocopy reveals an uncommon surface structure (Fig. 12). Usually, the surface is smooth, but in *H. narcissus* it shows a kind of compartmentation or facetting. This structure is also found in L_5.

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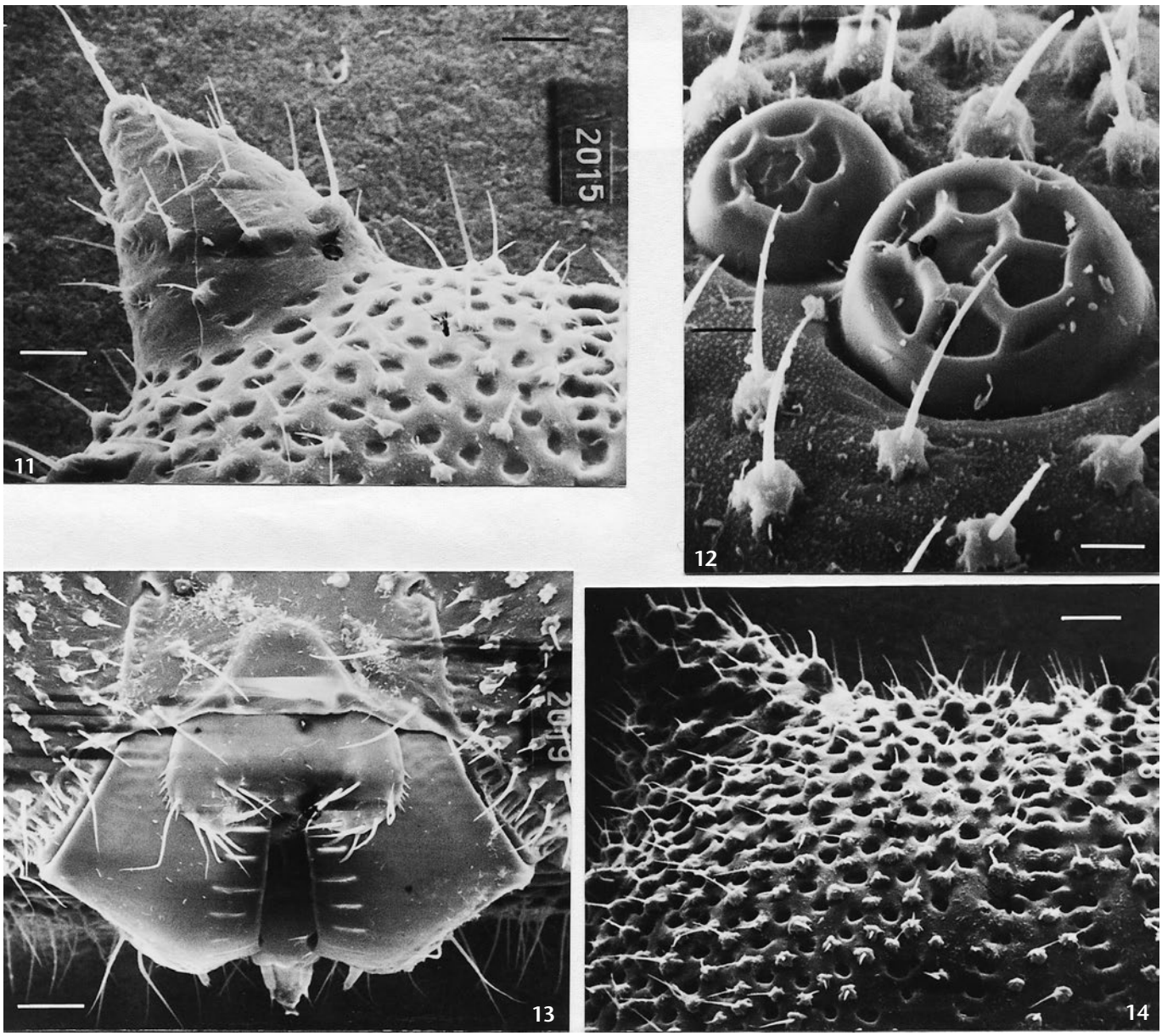

Figs. 11–14: Analysis of the surface structure of the larval head capsule of *H. narcissus* by scanning electron microscopy. **Fig. 11:** L_2, head process. **Fig. 12:** L_3, stemmata 2 and 3 (right). **Fig. 13:** L_3, frontal view with clypeus, labrum and mandibles. **Fig. 14:** L_4, details of the surface structure. — Bars represent: (14) 50 µm, (15) 20 µm, (16) 100 µm, (17) 100 µm.

L_5 larva: Freshly moulted, the colour of the head capsule and the body is light green. The former becomes light brown within one day and also the colour of the body changes to a brownish green, thus differing from all former instars. The subdorsal and lateral colour elements are light brown and constitute a clear ziczac line in the case of the subdorsalis (less pronounced in the epistigmatalis). The whole body is densely covered with short brownish setae which emerge from white chalazae altogether giving the larva a smooth appearance (Fig. 4). The most interesting structural feature of the L_5 larva, however, is the presence of densely arranged short trichomes on the dorsalis of the thoracic segments (Fig. 5). The stigmata show a specialized colouration. They are largely dark brown, but show a light triangle dorsally and ventrally. The head capsule is brown with numerous dark brown depressions between the conical chalazae. The dorsal scoli reach a length of about 500 µm and wear a lightly coloured stripe on their caudal surface which is connected to the subdorsalis of the body. Before moulting to the pupa, the L_5 larva has a maximum length of about 23.5 mm.

Pupa: Total length 11.3 mm. Typically for Mycalesina, the pupa is suspended by cremastal hooks. The orientation of the cremaster is nearly rectangular to the body. The light green pupa shows only sparse colour patterning (Fig. 6). The dorsal margin of the wing cases is outlined by a brown dorsal and a white ventral line. In the middle of the midleg, there is a dark brown melanized patch. Wing tracheation was analyzed in the freshly moulted pupa of *Henotesia narcissus* (Fig. 18). The branching pattern generally resembles that of other Satyrine species (Zeuner 1943, Roos 1986 and unpublished). The presence of 3 median branches and the absence of a cubito-median cross vein are characters of systematic and phylogenetic significance (see discussion).

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Discussion

Characters of the immature stages may well serve as a means to elucidate phylogenetic relationships within the Papilionoidea (see for example: Kitching 1984, DeVries et al. 1985, García-Barros 1987, Roos 1989). In this respect, we studied *Henotesia narcissus* as a representative of the satyrine subtribe Mycalesina in more detail. Although respective morphological data on most species of the Satyrinae are lacking, some conclusions can be drawn from available data.

According to the current opinion, the subtribe Mycalesina is a branch of the Elymniini further including the subtribes Elymniina, Lethina and Zetherina. This systematic assignment is based on investigations of the wing venation and the structure of the male foreleg (Miller 1968). However, character states of the immature stages of *Henotesia narcissus* described in the present paper do not confirm this systematic position of the Mycalesina. In contrast, the immatures of *H. narcissus* share several characters with the species of the tribe Ypthimina (Roos 1986, 1987a, b) and in part with the genus *Proterebia* Roos & Arnscheid, 1980 (Roos et al. 1984) whose systematic position is not clarified as yet but which may be closely related to the Ypthimina (Della Bruna et al. 2000). The following character states can be regarded as synapomorphies of the genus *Henotesia* and the Ypthimina:

(a) larval abdominal setae in L1 with clubbed tips and

(b) presence of dorsal trichomes on the prothorax of the last instar larva.

So far, these structural features have been found in the genera *Ypthima* and *Strabena* of the subtribe Ypthimina (Roos 1986, 1987a, b) as well as in the genera *Mycalesis* Hübner, 1818 and *Lohora* Moore, 1880 of the subtribe Mycalesina (Roos unpublished). Data from the literature show that dorsal trichomes are present in oriental *Mycalesis* and also *Palaeonympha* Butler, 1871 (Igarashi & Fukuda 1997), a genus of unidentified systematic position according to Miller (1968). Furthermore, clubbed setae are present in L_1-larva of the afrotropical ypthimine genus *Pseudonympha* Wallengren, 1857 (Roos unpublished). The two character states are obviously absent in species of the tribe Elymniini including the genera *Lethe* Hübner, 1819, *Elymnias* Hübner, 1818, *Parage* Hübner, 1819 and *Lasiommata* Westwood, 1848 as can be deduced from figures in Igarashi & Fukuda (1997) and own unpublished data.

Further characters shared by species of *Henotesia*, *Ypthima* Hübner, 1818 and *Strabena* are the spherical head processes in L_1 and the conically shaped head processes in L_2 to L_5. However, these are also present in other subtribes of the Satyrinae such as the Lethina, sensu Miller (1968) (Takahashi 1970, Igarashi & Fukuda 1997), and in a more developped form even in the Charaxinae (Henning 1988, Rydon 1971) which form the prospective sister group of the Satyrinae as suggested by DeVries et al. (1985). This latter view, however, is not supported by molecular systematic analysis based on rRNA sequences showing that the Charaxinae are more distantly related to the Satyrinae (Martin & Pashley 1992). Based on the data presented here, Mycalesina and Ypthimina appear to be phylogenetically closely related subtribes, a conclusion which has also been drawn in an earlier publication (Roos 1989). In two forthcoming publications, it will be shown that apart from *Henotesia* both above mentioned apomorphic characters are expressed also in further species and genera of the tribe Mycalesina (Roos, in preparation).

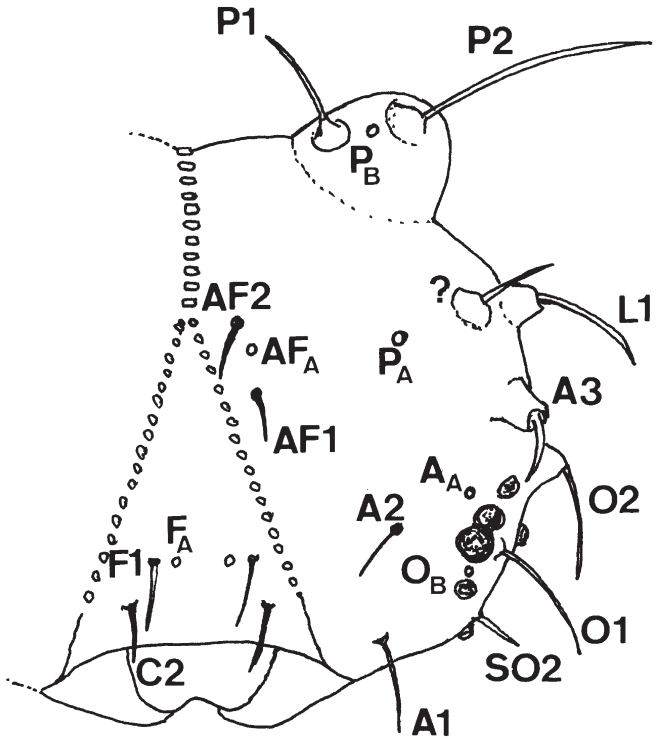

Fig. 15: Primary setae pattern of the L_1 head capsule in frontal view.

A phylogenetically relevant feature of the primary setae pattern of *Henotesia narcissus* may be the greater length of D_1 compared to D_2. This character state is not present in species of the Lethina genera *Pararge* and *Lasiommata* (Roos, unpublished) but is shared by species of the Ypthimina genera *Ypthima* and *Strabena* (Roos 1986, 1987b) and also by some other subtribes of the Satyrinae such as the Melanargiina (Roos 1979). In other (sub-)families of the Papilionoidea such as Pieridae and Nymphalidae: Danainae, however, D_1 is shorter than D_2 (Table 3). Further studies are needed to analyze this character in additional taxa of the Satyrinae. The presence of two subdorsal setae (SD_1 and SD_2) on the meso- and metathorax is not characteristic for the Satyrinae but is shared by other taxa of the Nymphalidae (Scott & Wright 1990). Another relevant chaetotactic character of the L_1-larva of *H. narcissus* is the absence of the clypeal seta C_1. Because C_1 is present in many closely and distantly related satyrines such as *Bicyclus* Kirby, 1871, *Hallelesis* Condamin, 1961 (Sourakov & Emmel 1997b), *Calisto* Hübner, 1823 (Sourakov 1996), *Ypthima*, *Par-*

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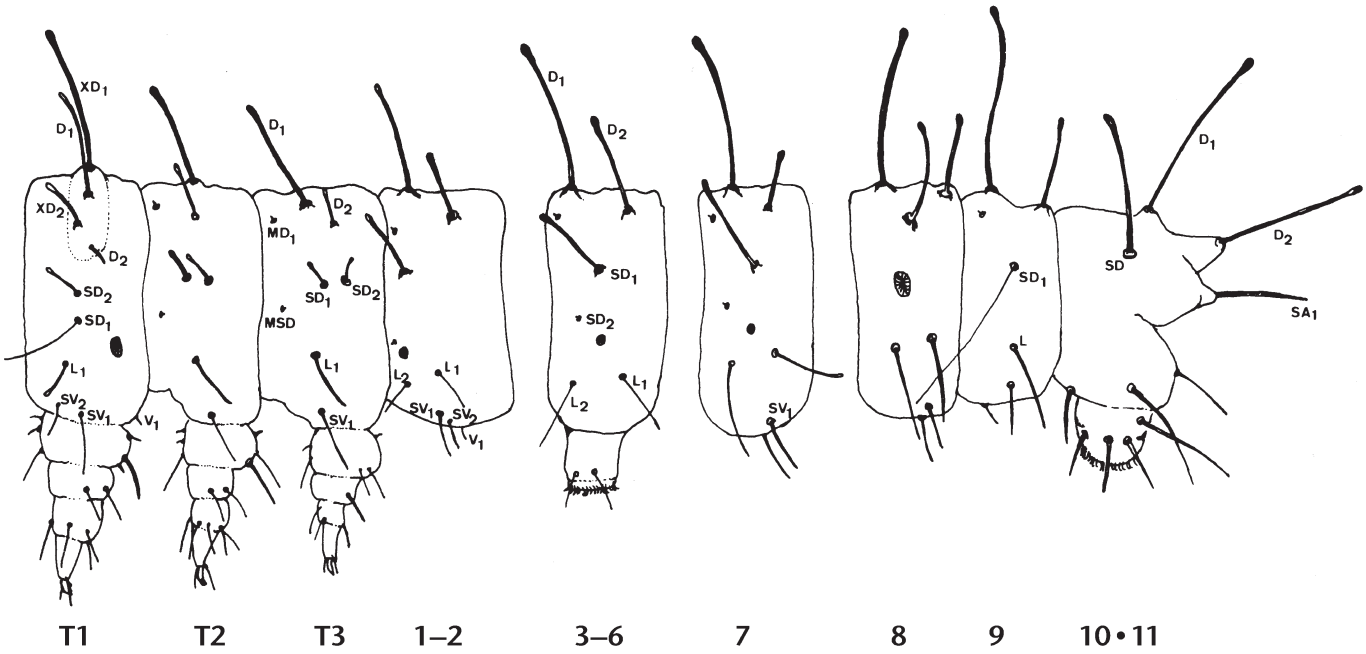

Fig. 16: Primary setae pattern of thorax and abdomen of *H. narcissus* (L1).

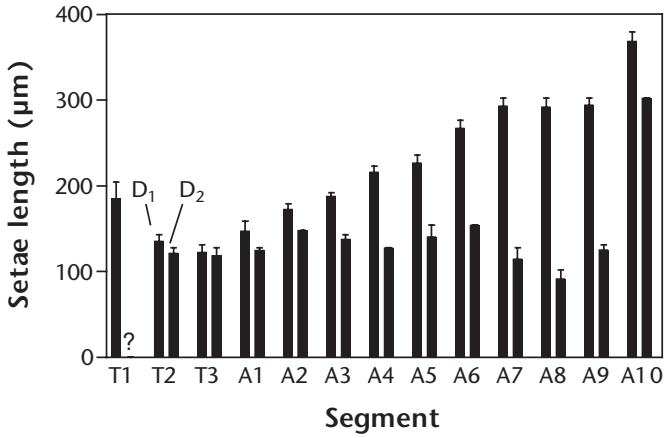

Fig. 17: Lengths of the dorsal body setae D_1 and D_2 on the thoracic and abdominal segments of the first instar larva of *H. narcissus*.

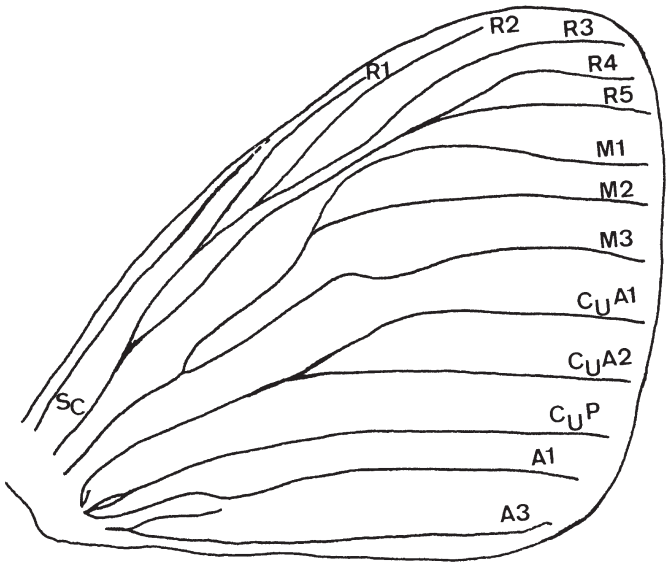

Fig. 18: Pupal forewing tracheation of *H. narcissus*.

arge, Lasiommata, Coenonympha Hübner, 1819, *Erebia* and *Pyronia* Hübner, 1819 (Roos unpublished) as well as in clear outgroups represented by the Pieridae (Yata & Fukuda 1980), the absence of C_1 has to be regarded as apomorphic in *H. narcissus*. Unfortunately, the closest relatives of *H. narcissus* have not been examined in this respect.

Homology assignment of the head capsule setae follows García-Barros (1987) who found a pattern in *Hipparchia fidia* which closely resembles that of *H. narcissus* described here. In both species, the epicranial setae P_1 are dislocated dorsally and are positioned on the scoli in *H. narcissus*. This dislocation appears to be typical for Satyrinae (Scott & Wright 1990). The designation of punctures A_A and P_A by García-Barros (1987) is doubtful and has been exchanged here. According to Hinton (1946), Brock (1990), Scoble (1995) and Nakanishi (1988) puncture A_A is closer to the stemmata than puncture P_A. This is in contrast to the conclusion of Kitching (1984) who positions P_A close to stemma 2 in the L_1-larva of *Danaus gilippus* (Cramer, [1775]) so that it lies ventrally of the line between setae A_2 and A_3. Even in the Pterophoridae where P_A and A_A show unusual positions, P_A lies dorsally of this line (Wasserthal 1970).

As in *Hipparchia fidia* and in *Erebia meolans* (de Prunner, 1798) (García-Barros 1987, Roos & Huck 1999), an epicranial seta with unidentified homology (marked with "?") has been found also in *H. narcissus* at a similar position. However, it appears not to be present in the genus *Lethe* of the tribe Elymiini as shown for *Lethe gemina zaitha* Fruhstorfer, 1914 by Yen & Jean (1995). Data from the literature show that this seta is not present in the Nymphalinae (Nakanishi 1988) and Danainae (Kitching 1984), but is obviously found in other Satyrines such as *Strabena tamatavae* (Boisduval, 1833) of the Ypthimina (Roos 1987b) and *Aphantopus hyper-*

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Table 4: Comparison of some characters of the primary setae pattern of several taxa. Data from: [1] García-Barros (1987), [2] Yata & Fukuda (1980), [3] Kitching (1984) and [4] Wasserthal (1970). Pro = prothorax; A9 = abdominal segment 9. + = yes; — = no; ? = not shown.

	Presence of L_2/Pro	Presence of L_2/A9	$D_1 > D_2$	SD_1/Pro specialized	SD_1/A9 specialized
Henotesia narcissus	—	—	+	+	+
Hipparchia fidia[1]	+	—	—	+	—
Ganduca harina[2]	—	?	—	—	—
Danaus gilippus[3]	+	+	—	—	—
Agdistinae[4]	—	—	+	—	—

Table 5: Comparison of some characters of Mycalesina, Ypthimina as well as Lethina and Elymniina. — Character states: + = yes; — = no, ± = poorly developped. S = synapomorphic. — Data for Elymniina/Lethina: [1] Igarashi & Fukuda (1997) for the genera *Elymnias* and *Lethe*. [2] Roos (unpublished) for the genera *Pararge* and *Lasiommata*.

Taxon	Mycalesina (*H. narcissus*)	Ypthimina	Elymniina Lethina
L_1, clubbed setae	S	S	—[1]
L_5, dorsal trichomes on prothorax	S	S	—[1]
Larva, stemma 3 enlarged	+	+	— (*Elymnias*) ± (*Lethe*)[1]
Pupal tracheation: fragmentary cubito-median crossvein	—	—	+[2]
Larval primary setae: $D_1 > D_2$	+	+	—[2]
L_1, head surfach with network of ridges	+	+	—

antus (Linnaeus, 1758) of the Maniolina (Roos 1981). It is possibly also present in the South African species *Stygionympha irrorata* (Trimen, 1873) (Ypthimina) (van Son 1955). Further analyses have to reveal whether this character proves to be synapomorphic for species of the subfamily Satyrinae (sensu Miller 1968). Nevertheless, the presence of this additional seta can be considered apomorphic in comparison to the Elymniini further confirming the position of the Mycalesina within the Satyrini and not within the Elymniini.

In all larval instars of *Henotesia narcissus,* stemma 3 is significantly larger than stemma 2. This character state is considered to be advanced and interpreted as a selectively advantageous feature in terms of improved optical perception (Sourakov & Emmel 1997a). The facette-like surface structure of the stemmata as observed by scanning electron microsocopy (Fig. 12) is interpreted in the same way (Sourakov 1997). Besides in Mycalesina, enlarged stemmata are also found in other satyrine taxa such as in the genera *Ypthima* (Roos 1986, Sourakov & Emmel 1987b) and *Strabena* (Roos 1987b) of the Ypthimina and in the genus *Hipparchia* of the Satyrina (García-Barros 1987). This feature is by no means characteristic for the Satyrinae as indicated by Scott & Wright (1990) but appears to be absent or only poorly developped in the Elymiina and Lethina as judged from figures in Igarashi & Fukuda (1997). Further examination is needed before the phylogenetic significance of this character can be assessed and used to determine the systematic position of the Mycalesina. Pseudo-facetted stemmata as defined by Sourakov (1997) are found in larvae of *H. narcissus* (Fig. 12) and are also observed in closely related genera such as *Bicyclus* and *Hallelesis* (Sourakov & Emmel 1997a) as well as in *Ypthima* (Sourakov & Emmel 1997b), *Erebia* (Roos & Huck 1999), *Strabena, Aphantopus, Pararge* and *Lasiommata* (Roos unpublished). Because we found these structures of the stemmata neither in life specimens nor in material preserved in 70% ethanol, we assume that they are artifacts of the drying process necessary for preparations destined for examination by SEM.

Characters of the pupal wing tracheation further confirm the notion that the Mycalesina are not closely related to the Elymniini and do not form a subtribe of the latter. Pupal wing tracheation has been extensively studied in Pieridae and was shown to be of diagnostic value on the generic level (Yata 1981). For satyrine butterflies, however, only a few data are available from the literature (Zeuner 1943, Roos 1986, Roos & Huck 1999). Judged from these data, there is apparently little variation in the pupal wing tracheation within the Satyrinae so that common patterns can be found in several genera and tribes. Own investigations revealed that the wing tracheation of *H. narcissus* (Fig. 18) resembles that of the satyrine genera *Erebia, Arethusana* de Lesse, 1951, *Aphantopus* Wallengren, 1853, *Pyronia, Ypthima* and *Strabena* but differs from that of the Elymniini genera *Pararge* and *Lasiommata* by the absence of a fragmentary cubito-median cross-vein (Roos unpublished).

In summary, there is strong evidence that the Mycalesina are not closely related to the Elymniini but form a

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branch of the Satyrini. Based on a number of common characters including synapomorphies we suggest that the Mycalesina are the sister-group of the Ypthimina. Although the data analyzed so far appear to be conclusive (Table 4), detailed analyses of further species of the Mycalesina and Ypthimina as well as of additional characters are necessary to come to a final conclusion concerning the phylogenetic relationship between the two subtribes. In this respect, the immature stages of *Ypthima kalelonda* Westwood, 1888 from Sulawesi, *Mycalesis phidon* Hewitson 1862 from Irian Jaya and *Lohora transiens* Fruhstorfer, 1908 from Sulawesi are currently investigated (Roos, in preparation).

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